CONTRIBUTIONS TO A KNOWLEDGE OF SOUTH AFRICAN OLIGOCHAETA.—Part I.

ON A PHREODRILID FROM STELLENBOSCH MOUNTAIN.

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The present paper deals with the anatomy of the reproductive system and the externals of a new Phreodrilid genus taken on the Stellenbosch Mountains during September, 1910.

This constitutes the first record of any representative of the family in Africa ; but at the same time the occurrence is not surprising, but rather expected, since representatives are found in all the other land masses of the Southern Hemisphere, including Kerguelen Island, which lie south of the parallel 30° S. We refer later to the significance of this distribution.

Several other essays during different times of the year both on the Stellenbosch Mountains and Table Mountain had proved fruitless in discovering either the same or different forms, since the first success ; and this was explained tentatively by us in a paper recently read before the South African Association for the Advancement of Science as being probably due to the fact that the worms mature during the spring and that they disappear from the pools during the hotter months of the year.

This explanation has been verified by the discovery of large numbers of another representative on Table Mountain during the past week.

Preliminarily we may note that the circumpolar distribution of the family is now complete, and we do not hesitate to remark that a detailed survey of the mountains above 3,000 feet and flanking the southern limits of the Karroo will furnish still many representatives of the family.

Not only does the new genus described herein prove interesting zoogeographically, but also is of important phylogenetic interest in explaining the spermathecal and male reproductive apparatus of such forms as Phreodriloides described by Benham from Mt. Koscisuko, New South Wales, and of a form described by one of us (E. J. G.) from Mt.

Wellington, Tasmania, but which was immature and in many ways so aberrant in regard to the spermathecal apparatus that it was deemed wise at the time of publication not to burden literature of the group with another new generic name.

There is now, however, no doubt but that the Tasmanian form constitutes a distinct genus for which the name Tasmaniaedrilus is now proposed—*T. tasmaniaensis*.

In view of the special distributional interest in the form under description, we propose the title *Gondwanaedrilus africanus* (gen. et sp. nov.).

GONDWANAEDRILUS, gen. nov.

Elongate body; ventral setae paired, one sigmoid, slender and simple, the other more markedly sigmoid, stouter, bifid; male pore in xii., female pore opening with male pore (?); spermathecal pores absent, spermathecal ducts opening into part of male apparatus.

Gondwanaedrilus africanus (gen. et sp. nov.).

Numerous individuals were obtained in a ditch on the plateau on Stellenbosch Mountain in association with Gammarus (an Amphipod), and Moss. No other vermian or invertebrate life was represented, and experience with the habitats of Phreodrilidae in Africa and other parts indicates that this fact has in all probability a marked significance, which we discuss later.

The individuals collected have an average dimension as follows :—

Length 20–22 mm.

Breadth ·8–1·0 mm.

Setae.—Each ventro-lateral group consists of two setae. One of these is slightly shorter, stouter, and more intensely sigmoid than the other; possesses a distinct modulus, and is strongly bifid at the free extremity. The other seta in each of these bundles has a simple pointed extremity.

The dorsal setae are exceedingly long, and capilliform with a distinct sigmoid yet faint curve. Each bundle carries three such setae. These setae are so easily broken in mounted and also preserved specimens that it is difficult in many cases to make out their distribution. However, they were traced forwards as far as segment iii.

Clitellum.—This structure extends through segments xii, xiii, and xiv.

In this paper we deal only with the Reproductive System, which constitutes the essential generic system in the group, for variation.

In all the specimens examined both ova and spermatozoa are abundant, indicating that fertilisation must take place during the spring.

The position of the gonads cannot be definitely stated, but can, at least in the case of the testes, be inferred within safe measures.

The male pores, as previously indicated, lie on each ventro-lateral region of segment xii.

The female pore could not be clearly made out, but observations suggest that in all probability it opens in common with the male pore, or, rather, immediately behind it.

In segments x, xi, there is a large median mass of developing spermatozoa, but no traces of masses of mature elements. Similarly there is an absence of such in the spermathecae, indicating that the breeding-time has not been reached.

The masses of spermatozoa in x, xi, resembling in position similar masses in Phreodrilidae, may be taken as indicating that the testes occupy the position usual in other genera.

Further, the funnel of the spermduct opens into xi. Masses of ova were found in xiv, xv. These clumps appear to be in close apposition and relation ? with the blood vascular system.

The spermathecae are paired structures situated in xiv immediately latero-dorsal to the alimentary canal. In longitudinal section each is elliptical. From the antero-ventral or ventral side the spermathecal duct passes down towards the ventral surface behind the septum separating xiii, and xiv. This duct instead of leading into the spermathecal chamber so that its wall becomes directly confluent with that of the chamber, becomes thickened so that its lumen communicates with that of the chamber at the summit of a large papilla which projects into the interior of the spermatheca.

The spermathecal duct on nearing the ventral surface pierces the septum and passes forwards into xiii. After a slightly tortuous course it then ascends obliquely and forwards to open into the posterior end of a cylindrical chamber, which is an extension backwards and dorsally from the penial chamber.

The most noteworthy feature about the spermathecae is the marked thinness of the wall, at least in part, when compared with the wall of the corresponding chamber in other genera such as Phreodrilus and Astacopsidrilus. The posterior and dorsal wall is so thin and indistinct in our specimens that it is difficult, except that assistance is rendered by the thicker anterior and ventral part of the wall, to make out histological details.

On first examination we were struck with the great resemblance between the wall of the spermatheca in part, and the inter-segmental septa, which suggested that these chambers were of the same nature and origin as those found in Eudrilidae.

The histology of the wall is better understood by a study of the spermathecal duct. The wall of this tube is composed of three layers :—

(*a*) The lining layer consists of large cuneate cells bounding a

central lumen, with granular protoplasm and a large basally situated nucleus.

(*b*) As in the case of the spermathecal ducts in Astacopsidrilus, &c., there is a well-developed circular musculature.

(*c*) The outermost layer, which is greatly exaggerated in the figure, consists of a flattened and indistinct coelomic epithelium.

The duct on approaching the spermatheca becomes confluent at first with a horn given off from the antero-ventral portion of the spermathecal chamber. It pushes itself into the ventral side of this horn as represented in the figures so that it and the crescentic horn become encased in a common circular musculature. Eventually the duct becomes free in the cavity of the horn, but is now devoid of a musculature, consisting solely of cuneate granular cells. It ceases at the line of junction between the horn and main part of the spermatheca.

The horn thus envelops the duct as a sheath.

The wall of the horn consists of a lining layer of epithelial cells which are loosely arranged, pyriform or lobose, and a distinct outer circular musculature which is confluent with that of the spermathecal duct.

The epithelium of large lobose cells is continued over the interior of the anterior and ventral wall of the main part of the spermatheca. These cells are very large at the commencement of the spermatheca.

This strong epithelium withers away posteriorly, especially along the dorsal wall of the chamber, to such an extent that with a fairly high objective it is difficult to decipher whether this very thin dorsal wall is constituted by a very much flattened epithelium or by a basement membrane from which the epithelial cells found in the anterior and ventral regions have dropped away. This latter idea is suggested by the loose nature of the large lobate cells in the anterior region of the sac and in the horn of the same, and would seem to be the most satisfactory way of explaining the histological differences between the different regions of the spermatheca, and between the spermatheca in part in Gondwanaedrilus and that of other Phreodrilidae such as Phreodrilus and Astacopsidrilus.

The circular musculature found external to the epithelium of the spermathecal duct and spermathecal horn extends for a very short distance external to the epithelium of the anterior part of the chamber, but soon dies out.

In this region also both dorsally and ventrally there are the remains of a loose epithelium, represented by pear-shaped cells, isolated, and much smaller than the lining epithelial cells.

The spermiducal gland is a sigmoid structure, being made up by an axial portion directed antero-dorsally and postero-ventrally, an anterior part running ventrally from the anterior extremity of this, and an

ascending posterior portion. The anterior descending moiety lies immediately behind the septum separating xi and xii.

The sperm duct leads backwards from the funnel through the septum xi, xii, and becomes intricately coiled ventrally to the anterior limb and axis of the spermiducal gland. It then passes upwards and backwards to open into the extremity of the posterior ascending part of the spermiducal gland.

The penis projects for some distance into the ventral moiety of the large chamber into which the male pore leads, and its cavity eventually opens into the same.

The large chamber consists of a vertical half which is definitely marked off from a posterior portion which lies behind the entrance of the penis, and with the exception of its anterior extremity lies horizontally. This posterior portion lies partly in segments xii and xiii, and receives at its free posterior extremity the spermathecal duct.

The penis is an elongate pear-shaped structure, its basal portion being attached to the anterior or antero-dorsal wall of the large sac into which the male pore opens. The attachment lies just where the posterior moiety of this sac passes backwards, and this gives at once the impression that this posterior part is of the nature of a diverticulum from the vertical portion which leads to the exterior.

The penis resembles histologically that of Astacopsidrilus in the main, but the chitinous band external to the lining epithelium is absent.

The wall of the penis is composed of three layers :—

(*a*) The inner epithelium is composed of large cells, with markedly granular protoplasm, and with a large spherical nucleus situated towards the base.

(*b*) The middle layer of muscle fibres becomes gradually thicker towards the base of the penis where it reaches its maximum. The area occupied by the musculature is very spongy in the basal region, but this may be due to post-mortem changes or imperfect preservation.

(*c*) The outermost layer is composed of epithelial cells which become much more important gradually from the apex to the base of the penis. Except in the immediate region of the apex of the penis this outer layer is heavily folded, and resembles both in this respect and in the nature of its component cells the lining layer of the sac into which the penis protrudes.

The large sac into which the male pore leads and which contains the penis has a wall composed of three elements :—

(*a*) The inner epithelium is heavily folded, and projects into the lumen of the sac in the form of large blunt villi. Each villus is composed of a number of small squarish cells with a centrally situated nucleus. Into the heart of each villus there project muscle fibres which externally mingle with those of the second layer.

(*b*) The middle layer is composed of muscle fibres, oblique and circular in direction.

(*c*) The outermost layer is composed of loose parenchyma-like cells which in places are very indistinctly made out. This is in all probability due to the state of preservation.

The only other member of the Phreodrilidæ possessing any structure resembling this sac is Phreodriloides, where we find a chamber into which the male pore and the spermduct lead.

This structure has until now been imperfectly understood, since the absence of true spermathecae in Phreodriloides raised special difficulties. Benham termed it tentatively an "autospermatheca," or, at least, regarded the portion lying behind the entrance of the spermduct as corresponding to a specially developed spermathecal apparatus, rather than that the spermathecal pore had moved forwards and become coincident with the male pore.

There can be no doubt that in the rejection of the latter explanation Benham was quite correct.

The anatomy and histology of the form under description show clearly that the large chamber is nothing more than the greatly enlarged penial sheath. Its histology is fundamentally similar to the normal penial sheath of such forms as Astacopsidrilus and its relation to the penis corroborates this idea.

The "muscular sac" of Phreodriloides is undoubtedly the homologue of the posterior horizontal portion of this sac in Gondwanaedrilus, and both of these structures are posterior outgrowths of the penial sheath. The so-called penial chamber of Phreodriloides and the "muscular sac" have become differentiated histologically along different lines, the former becoming in part glandular, the latter becoming heavily muscularised. Both, however, represent portions, ventral and dorsal respectively, of the large sac of Gondwanaedrilus.

A glance at the figures of this structure in both genera will quickly convince one of the homology.

Anatomically, special interest centres round the spermathecae and male reproductive apparatus since we now have a definite explanation of the peculiar modification of these in Phreodriloides.

In order to make this perfectly clear we will orient ourselves by taking in assumption as normal the condition of these organs in Phreodrilus.

In this genus the spermathecae are well-developed paired structures opening independently to the exterior, and provided with a strong definite granular and glandular epithelium. This applies to all the species of the genus.

In Astacopsidrilus the spermathecae may remain separate or may communicate with each other, but the walls retain the same nature of

that of Phreodrilus. In this genus, however, a most important modification is wrought in that the spermathecal ducts open, not to the exterior, but into a thin-walled sac—an ovisac—from which the oviduct leads definitely to the exterior, opening in the position or segment characteristic of Phreodrilus. The structure of the spermiducal gland and male apparatus resembles fundamentally that of Phreodrilus. The communication between such a "true" spermatheca and the female duct is unique.

In Gondwanaedrilus we find definite paired spermathecae which occupy the typical position but which communicate with the male chamber. This is an exceedingly interesting counter-condition to that in Astacopsidrilus.

As has been pointed out previously in this paper in considering the structure and histology of this organ its wall differs very much from that of Phreodrilus and Astacopsidrilus. The thinness of the wall posteriorly suggests at first that here the spermathecae are of the same nature and origin as in the Eudrilidae. This view we cannot accept, however, since the antero-ventral portion of each chamber near its junction with the spermathecal duct is lined with thick pear-shaped cells recalling similar cells in connection with the spermiducal glands to which histologically there is a general resemblance in Oligochaeta in general. The significance and importance of this view will be seen when considering Phreodriloides.

Lastly, the extension of the penial chamber upwards and backwards beyond the entrance of the penis to meet the spermathecal duct is important since this extension undoubtedly represents the muscular sac or "autospermatheca" of Phreodriloides.

In Tasmaniaedrilus one of us (E. J. G.) noted a series of unpaired and disconnected chambers with thin walls, and recognised such as the remains of spermathecal structures. The structure of the wall in the spermathecae of Gondwanaedrilus no longer leaves doubt concerning the correctness of this view. In all probability in Tasmaniaedrilus we see the remains of an evanescent spermatheca devoid of ducts.

In Phreodriloides it is now perfectly clear that the true spermathecæ have disappeared, and that the so-called "autospermatheca." corresponds to the extension of the penial chamber in Gondwanaedrilus.

The various modifications of the spermathecae are shown in the table below :—

Phreodrilus	Spermathecae and pores distinct. Wall distinctly glandular.
Astacopsidrilus	Spermathecae distinct, but ducts communicating with female duct. Wall distinctly glandular.

Gondwanaedrilus	Spermathecae distinct, but ducts communicating with male penial chamber.
Tasmaniaedrilus	Spermathecae evanescent and ducts absent. Wall thin and non-glandular.
Phreodriloides	Spermathecae and ducts absent.

It will be seen that we have now an undoubtedly complete anatomical series, and that the family which at first known only by the genus Phreodrilus was considered so unique in regard chiefly to its setae and spermathecae, can be split into genera whose most marked differential characters concern both these structures.

Again, it is quite clear that Phreodrilus with its well-developed spermiducal gland, glandular spermatheca, and spermathecal ducts opening directly to the exterior, approaches more closely than any of the other genera to the ancestral Phreodrilid stock.

Remarks.

The distribution of the family has been very interesting up to the present time in view of the limitation to the southern portion of the Southern Hemisphere, and also of its restricted habitat in these regions.

That the group does possess a great phylogenetic value will, we think, be conceded by all workers on the Oligochaeta, and the fact that their occurrence in South Africa and further in the mountainous region only was deduced by one of us several years ago is, at least, not inconsistent with this idea.

The fact that the well-searched parts of the Northern Hemisphere where under varied bathymetrical conditions the Oligochaetan fauna has been well investigated by many of the foremost workers on the group, have not revealed any Phreodrilid representatives—and the same applies in the case of the tropics—may very reasonably be interpreted as indicating the restriction of the family to the area including the various parts where they are now known to occur.

In a previous paper it was noted by one of us that the habitat appealed in its peculiar conditions as a significant fact.

All the Phreodrilidae yet discovered and described are inhabitants of cold areas, with the exception of Astacopsidrilus which, however, can be neglected here since its peculiar external appearance bound up with its unique association with the Crayfish—Astacopsis—makes it appear as being *sui generis*, and explains its bathymetrical and exceptional distribution. The various forms, if not inhabiting areas with a constant low temperature as in the Falkland Islands, occur on mountains exceeding easily 3,000 feet, and we now know that the worms appear in the pools only during the colder seasons of the year.

These remarks may be construed as signifying one of two conclusions :—

(*a*) The living Phreodrilidae are the descendants of an old cold climate ancestral stock which once inhabited the southern lands, and are now restricted to areas where these conditions are now attained; or—

(*b*) The Phreodrilidae are the remnants of a stock which has been unable to meet the demands for existence under normal and temperate conditions, and consequently have taken up an abode in places where the struggle for existence is far less keen.

Before discussing these conclusions we will mention several facts which will tend to make the issue more easily understood.

Firstly, the Phreodrilidae undoubtedly show marked affinities, when phylogenetically considered, with the Lumbriculidae, and the latter are as truly restricted to the Northern, as the former to the Southern Hemisphere.

Secondly, it would appear that the Phreodrilidae are not capable of transmigration across sea barriers, as are so many of the terrestrial Oligochaeta. They do not meet with the same chances of migration at the hands of man like many terrestrial Oligochaeta—a fact which is explained by their habitat, and that the chief medium serving for conveyance in the hands of man is either soil or water ; and which is supported by the absence of Phreodrilidae except in the restricted habitats mentioned above, and by the fact that as yet no species is known as being common to any two of the land areas where the family is represented. In this connection we cannot but point out that in no division of the Invertebrata are the species more valid since they are framed without exception not only on exceedingly well-marked external differences in connection with setae, etc., but also on peculiarly accentuated internal differences. There is no room for synonymy in any of the group.

The restriction of the family to the Southern Hemisphere certainly finds its parallel in the case of many other groups, but it would seem that no explanation other than that of the existence at one time of a direct connection between the continents of the Southern Hemisphere is satisfactory. The Lumbriculidae which occupy a corresponding phylogenetic importance are as truly restricted to the Northern Hemisphere, and thus we are led to conclude that each group has been evolved in the respective hemispheres. This being the case, we must then regard the existing members of the family as the descendants of an ancient Phreodrilid ancestor which may have flourished as early as, if not earlier than, Permo-Carboniferous times on ancient Gondwanaland.

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